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SEED VIABILITY AND GERMINATION BEHAVIOR OF THE DESERT SHRUB *ENCELIA FARINOSA* TORREY AND A. GRAY (COMPOSITAE)

Pamela E. Padgett[1]
Pacific Southwest Forest and Range Experiment Station, USDA-FS, Forest Fire Laboratory, 4995 Canyon Crest Dr., Riverside, CA 92507

Lucia Vázquez
Department of Plant Biology, Cornell University, Ithaca, NY 14853

Edith B. Allen
Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124
Fax: (909) 787-4437

Abstract

Restoration and revegetation of arid and semi-arid landscapes requires an understanding of the targeted environmental conditions, physiological requirements of the plant species, and horticultural tools available to complete the project. *Encelia farinosa* Torrey & A. Gray is a shrub widely adapted to desert and coastal sage shrublands. It is often included in seed mixes intended for revegetation of disturbed arid lands. However, the successful establishment of shrubs in wild lands and the ability to grow *Encelia farinosa* under horticultural conditions has been hampered by poor germination percentages, typically 2–5%. In this study, we endeavored to establish the source of germination failure and to test methods for increasing germination. We found that nearly half the seeds collected from field sites or donated from a commercial source were not viable. The seed coats were either completely empty or contained embryos and endosperm unresponsive to the metabolic indicator Triphenyl-tetrazolium chloride, indicative of dead tissues. Of the remaining seeds, soaking seeds in gibberellic acid, a well-known germination stimulant, enhanced germination. The ecological significance of such a large number of non-viable seeds is not understood, but for restoration purposes, the data suggests pretreatment with gibberellic acid may increase establishment of genetically mixed stands.

Encelia farinosa Torrey & A. Gray (Compositae) is an arid-zone shrub with floral structures that are typical of the family. The seeds are flattened achenes similar in appearance to small sunflower seeds. The edges of the achenes are ciliate and the faces are slightly pubescent which may aid in animal dispersion (Keator 1994). This species is native to the deserts of California, Utah, Arizona, and New Mexico as well as parts of northwestern Mexico (Clark 1993). It is also a common component in the drier sites of the Mediterranean coastal sage scrublands of southern California and tends to occupy alluvial fans and rocky aprons, especially on south facing slopes (Clark 1993; Keator 1994). *Encelia farinosa* is facultatively drought deciduous, normally loosing its leaves during dry summers. It will, however, remain evergreen or flush new leaves when even small amounts of rainfall or irrigation are introduced (Smith and Nobel 1986; Ehleringer and Cook 1990). The ecophysiology of this plant is among the best studied of the desert-adapted species. This is, in part, because of its abundance in nature and its large and accessible leaves (Nobel et al. 1998). However, where disturbance has eliminated this species, little is known about the reestablishment of natural stands.

The understanding of restoration and revegetation processes in disturbed arid and semi-arid habitats is becoming more important as human utilization and the intrinsic value of arid ecosystems continue to increase. Adjustments in desert management such as abandonment of military installations, curtailing of mining operation, restrictions in livestock utilization and heightened interest in the recreational value of deserts have increased the interest in reestablishment of native desert vegetation (Bainbridge et al. 1995). In related semi-arid ecosystems such as coastal sage scrub, the listing of many plant and animal species as rare, threatened, and endangered has driven legal requirements to restore appropriate habitats (Bowler 1990; Minnich and Dezzani 1998). However, re-establishment and management of native arid and semi-arid vegetation has proved challenging due to severe environmental stresses such as water limitations and high temperatures. (Mooney 1982; Call and Roudy 1991; Bainbridge et al. 1995). Many unique adaptations allowing plants to germinate and survive under these conditions have evolved. Among those adaptations are germination strategies designed to inhibit or trigger emergence depending on environmental conditions (Went 1948; Bowers 1994).

[1] To whom correspondence should be addressed e-mail: ppadgett@citrus.ucr.edu

The reported germination percentages for *Encelia farinosa* are typically 2–5% under ordinary horticultural conditions (Emery 1988; Szarek et al. 1996). Although some work has been published regarding germination under natural field conditions (Went 1948; Bowers 1994), less is known for horticultural approaches. The ability to raise seedlings under horticultural conditions for scientific study, ornamental use, or for restoration purposes is important for progress in these endeavors. It may be even more important in restoration projects where natural germination and seedling survival is poor, or where rapid revegetations is preferred. *Encelia farinosa* is easily propagated from stem cuttings (Joshua Tree Nursery personal communication), but concerns about overly uniform genetic backgrounds in clonal populations makes this a less desirable option in fragmented habitats where loss of genetic diversity could lead to local extinctions.

The objectives of this work are twofold: 1) to determine the causes of low germination in seeds from natural populations and from commercial sources and 2) to identify readily available seed treatments for enhancing germination.

Materials and Methods

Seed collection and storage. Three seed sources were used: two collected from local populations and one donated from a commercial source. The locally collected populations were from two coastal sage sites, Box Springs Mountain and Lake Skinner, approximately 70 km apart in Riverside County, CA. The collected seeds from each site were pooled from many individuals in the population. The commercially available seed was acquired from S&S Seed in Carpinteria, CA and consisted of a mixed population of individuals collected from southern California. Harvesting and storage of the S&S seed is presumed to be optimal for commercial purposes. Seeds from the three different sources were divided into two groups; one was stored in a standard refrigerator at about 5°–10°C and the other group was stored in the dark at room temperature. The seeds were stored in paper bags and were neither cleaned nor sorted prior to storage.

Prior to planting, each seed was selected individually after visual inspection under a dissecting microscope. Seeds containing obvious defects, signs of predation or those smaller or larger than the population means were rejected. Acceptable seeds were pooled and redistributed as required for each experiment.

Viability determination. Seed viability was tested in the bulk population prior to germination testing, and in the ungerminated seeds following the germination tests using a Triphenyl-tetrazolium (TZ) staining technique. For the evaluation of embryo viability in the bulk seed populations (Box Springs, Lake Skinner and S&S Seed), 200 uniform seeds from each source were selected for intact, uniform appearance and then divided into 10 replicates of 20 seeds. The seeds were soaked in a 1 mM $CaCl_2$ solution at 37°C for 1 hr to initiate imbibition and then dissected for TZ staining.

For evaluation of viability after the petri dish germination trial, the ungerminated seeds were scored for the presence or absence of fungal contamination and the uncontaminated seeds dissected for TZ staining. In the post-germination viability tests, the seeds were scored by the following criteria: fungal contamination, presence or absence of embryo and endosperm, and viability stain. A similar approach of scoring ungerminated seeds from the vermiculite pots studies was attempted in order to compare the differences in germination between these studies. However retrieval of the ungerminated seeds from the vermiculite pot studies was unsuccessful.

Triphenyl-tetrazolium chloride (TZ) staining is an indicator of metabolic activity. The method used was adapted from Das and Sen-madi (1992). For staining, the seed coats were removed from each seed and the exposed embryo and endosperm were placed into a solution of 0.5% TZ dissolved in 0.1 mM $CaCl_2$. Stain-treated seeds were incubated in a water bath at 50°C for 30 minutes and then inspected under a dissection microscope. Viable seeds indicated metabolic activity by the presence of a strong pink/red coloring of the embryo. Occasionally staining of the endosperm, but not the embryo, was observed. When this occurred the seeds were not scored as viable. The intensity and degree of staining varied markedly from seed to seed, but there did not seem to be any correlation between magnitude of staining and the seed source, age, or germination potential.

Germination percentages on different substrates. Germination percentages were determined by two methods, petri dishes lined with germination blotter paper and in pots containing sterile vermiculite. The petri dish method is typical of standard germination tests and vermiculite is typically used for seedling establishment prior to transplanting into potting soil. Seeds to be tested in petri dishes were transferred after visual inspection to disposable petri dishes lined with 2 layers of blotter paper. The blotter paper was premoistened to saturation with 1 mM $CaCl_2$ and any standing solution was removed. Twenty seeds were placed in each dish and the dishes were sealed with parafilm to reduce evaporation. The petri dishes were placed in an incubator under low light (approximately 50 $\mu mol\ m^{-2}\ s^{-1}$) at a constant temperature of 25°C. Each dish was opened every two days to enumerate germinated seeds and to replace the $CaCl_2$ when necessary. Emergence of the radical was scored as germination and once counted, the germinated seed was removed. The evaluations typically ran 10 days after which further germination was infrequent. At

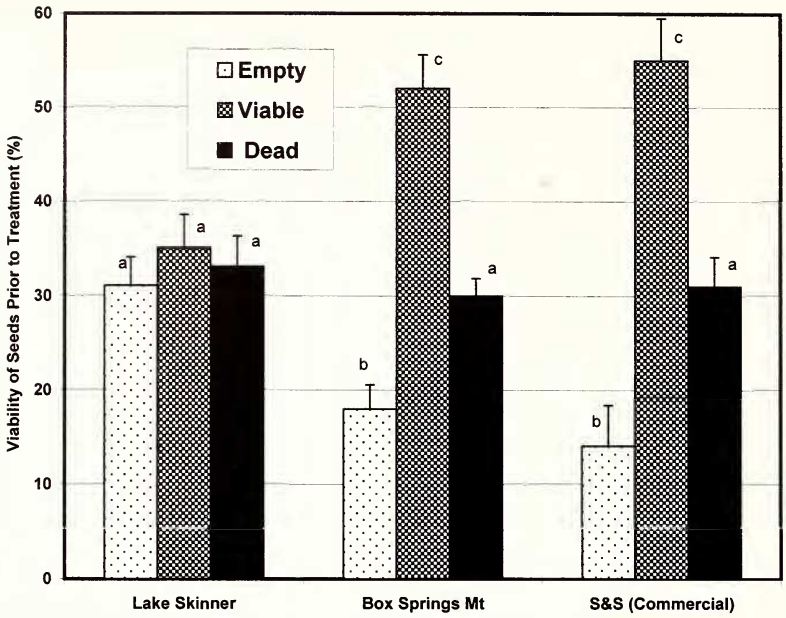

FIG. 1. Percent viability as determined by tetrazolium staining. Three bulk populations were evaluated: two collected locally and one donated by a commercial source. The seeds were stored at 5–10°C for 6 months prior to testing. Letter designations denote significant differences at the $P < 0.01$ level and error bars indicate SEM.

the conclusion of the evaluations, the remaining seeds were inspected as described above.

To estimate the germination percentages in vermiculite, following visual inspection seeds were transferred to 4 inch pots partially filled with moist, sterile, expanded vermiculite (McConkey Co., Sumner, WA). The pots were kept in a glasshouse with an average light level of two-thirds full sunlight and a temperature regime of 80°F days, 65°F nights. Complete germination generally required 2 weeks. Seedlings were not removed until the end of the experiment whereupon they were transplanted into potting soil. The success of transplanting was 100%.

Germination responses to chemical treatments. Seeds were treated with the following chemical solutions that have been reported to enhance germination in some plant species: 0.5 mM $Ca(NO_3)_2$, 1 mM $CaCO_3$, and 100 ppm gibberelic acid. One mM $CaCl_2$ was used as a control (Bewley and Black 1994). Some experiments included a combined 0.5-mM $Ca(NO_3)_2$ and gibberelic acid treatment. Each experimental unit contained 20 seeds and was replicated 5 times per treatment using both petri dishes and vermiculate as substrates.

Preliminary experiments investigated chemical treatment, incubation temperature, and duration and appropriate germination substrate. For determination of exposure time, seeds were soaked in solutions at room temperature or at 37°C for 0.5, 1, 3 or 6 hours. The elevated temperature proved more reliable than room temperature (data not shown) and soaking the seeds for more than 3 hours was fatal in most cases (data not shown). Germination trials using native soils or potting media produced poor results regardless of the treatments applied, therefore experiments were conducted using standard petri dish and vermiculite techniques only. Once the parameters were established, the experiments described were conducted once for the locally collected seed source and twice for the commercially available seeds. Data shown are from commercial source experiments, because the results would be easiest to replicate by others.

Statistical analysis. Germination percentages were analyzed by one-way ANOVA using SigmaStat, version 2.0 by Jandel Scientific Software (San Rafael, CA, USA). Statistical significance of the differences were generally set at $P < 0.01$, but the specific rejection criteria of each experiment is indicated in the text.

RESULTS

Seed viability—untreated seeds. Dissection and TZ staining indicated that a large proportion of the *Encelia farinosa* seeds were either empty (absence of endosperm) or contained a dead embryo (Fig. 1). A comparison of the three seed sources indicated no significant difference in the percent of seeds with a dead embryo, approximately one-third of the total. However, seeds collected from Lake Skinner had a significantly greater ($P < 0.01$) percentage of empty seeds than the other two sources even though the outer appearance of the seed was normal. No significant difference in the percentage

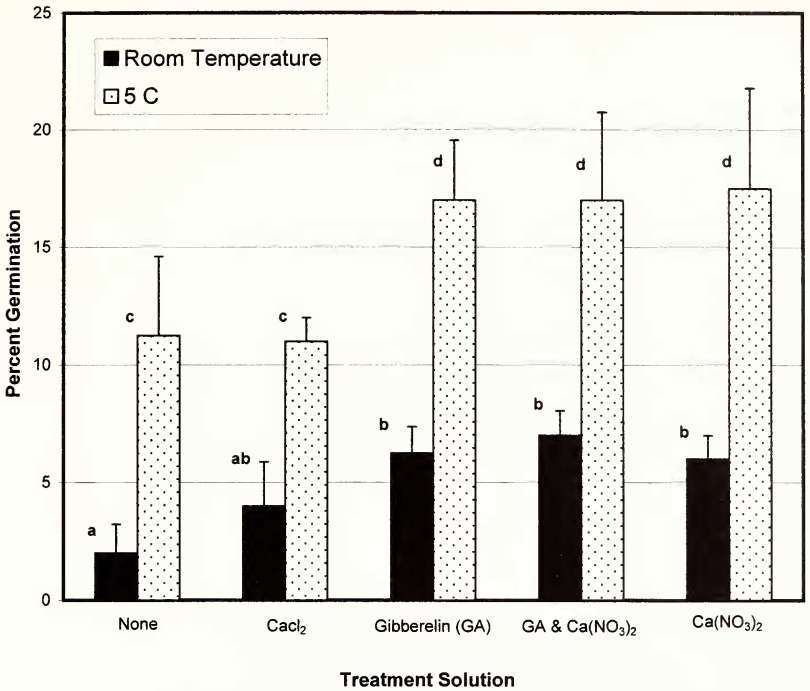

FIG. 2. Comparison of the effects of storage temperature on germination response to four common seed treatments. Data shown is from seeds donated by S&S Seeds, but all seed sources indicated similar responses. Seeds were soaked 30 minutes at room temperature in each of the solutions indicated. Please refer to the materials and methods for solution details. Letter designations denote significant differences at the $P < 0.01$ level and error bars indicate SEM.

of empty seeds was found between the Box Springs Mt and the commercial seed sources (18% and 14% respectively). Seeds collected from Lake Skinner showed the lowest percentage of viable seeds compared to the Box Springs and commercial sources. On average, only 35% of the seeds collected from Lake Skinner would be expected to germinate as compared to slightly more than 50% from the other two sources.

Effect of storage temperature and chemical treatment on germination. Germination was significantly affected by storage conditions. Seeds stored for six months in a standard refrigerator held to approximately 5° to 10°C exhibited two to three times greater germination percentages than seeds stored at room temperature (Fig. 2). Under both storage regimes, seeds were placed in paper bags, kept as dry as possible and were not deliberately stratified (Emery 1988; Bewly and Black 1994).

The response to commonly used germination stimulants indicated trends of greater germination with chemical treatment under both room temperature and cold storage regimes. Seeds stored at room temperature (black bars, Fig. 2) germinated at significantly higher percentages ($P < 0.01$) when soaked in gibberellic acid, $Ca(NO_3)_2$ or a combination of gibberellic acid and $Ca(NO_3)_2$. The $CaCl_2$ treatment resulted in an intermediate response that was not significantly different from untreated seeds, or from seeds receiving gibberellic acid, $Ca(NO_3)_2$ or a combination of gibberellic acid and $Ca(NO_3)_2$. Seeds stored under cold conditions (shaded bars) exhibited germination percentages that fell into two classes. Mean germination percentages were identical for untreated seeds and seeds treated with $CaCl_2$. Seeds soaked in $Ca(NO_3)_2$, gibberelic acid or a combination of both solutions showed an average of 50% greater germination than those untreated or soaked in $CaCl_2$. Analysis of variance identified significant differences between the germination percentages of untreated seeds and seeds soaked in gibberellic acid, $Ca(NO_3)_2$ or a combination of gibberellic acid and $Ca(NO_3)_2$ at the 95% confidence interval. No difference in germination between the untreated seeds and the $CaCl_2$ treated seeds was noted, and there was no difference among the gibberellic acid and NO_3^- treatments.

Chemical treatments—petri dish tests. Soaking seeds in commonly used germination stimulants resulted in a mix of germination responses (Fig. 3). Seeds were selected from the refrigerator-stored batches, and soaked for 30 minutes, 1 or 3 hours at 37°C. In the treatments using $CaCl_2$ and $Ca(NO_3)_2$, differences in the soaking times did not result in any significant differences ($P < 0.01$) in germination percentages. In the treatments using $CaCO_3$ and gibberellic acid, however, an increase in the soaking time suggested a trend in increased

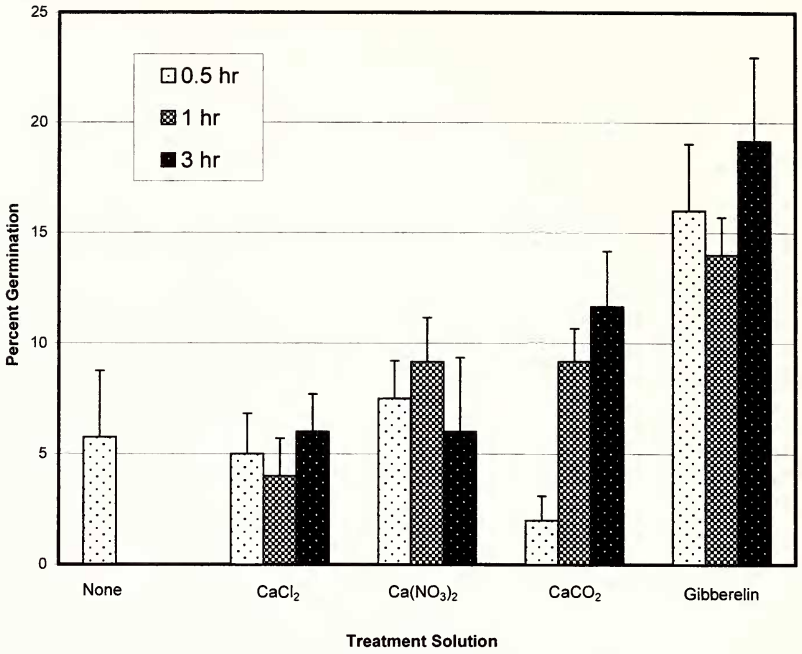

FIG. 3. Evaluation of chemical treatments and exposure times for enhanced germination of *Encelia farinosa* seeds incubated in petri dishes. Data shown are from commercially available seeds stored under cold conditions. Similar responses were observed for seeds collected from local sites.

germination. On average, gibberellic acid doubled germination as compared to $CaCl_2$, $CaCO_3$, and $Ca(NO_3)_2$. Germination percentages among these three calcium salts were not significantly different. Contrary to the results shown in the storage temperature experiment (at 5°C; Fig. 2), $Ca(NO_3)_2$ did not result in any clear, significant increases in germination as compared to the $CaCl_2$ treatment. A comparison of germination percentages in seeds treated with $CaCl_2$ or $Ca(NO_3)_2$ for 1 hour resulted in a significant difference at the $P < 0.1$ level suggesting a slight, but inconsistent response to nitrate.

Maximum germination even in the gibberellic acid treatment was still less than 20% and between 5% and 10% for most of the other treatments. This is considerably less than the 50% maximum germination indicated by evaluating the bulk seed populations (Fig. 1).

Seed viability—ungerminated seeds. Viability tests performed on seed that did not germinate after the 10 days in petri dishes indicated that between 50% and 60% of those seeds contained a dead embryo and between 5% and 10% of the seeds coats were empty (Fig. 4). Fungal infection, presumably from seed borne spores, claimed 20% to 30% of the seeds, leaving approximately 5% of those ungerminated seeds with viable embryos.

Chemical treatment—vermiculite pots. The overall pattern of enhanced germination with chemical treatment observed in the petri dish trials was replicated in the pot studies (Fig. 5). As with the petri dish trials, there was no a clear pattern of increased germination rate with increased soaking times in the different chemical treatments. Germination in general, however, was better in vermiculite than in the petri dishes. On average, vermiculite produced a 50% increase in germination in the $CaCl_2$ treatment, a 3-fold increase in $CaCO_3$, a 3-fold increase in $Ca(NO_3)_2$ treatment, and a little more than 2-fold increase in the gibberellic acid treated seeds over the petri dish germinations. Germination remained significantly higher in the gibberellic acid treated seeds, but the trend was for seeds soaked for 3 hours to yield less than seeds soaked for 1 hour. Seeds soaked in $CaCl_2$ for 3 hours had significantly lower germination percentages than most of the other treatments.

DISCUSSION

Encelia farinosa is not known to have any germination barriers such as those reported for many arid and semi-arid species (Emery 1988; De Hart 1994; Kigel 1995), even though germination rates of 2 to 5% are typically encountered. The low germination rate of *Encelia farinosa* has made sexual propagation of this species problematic for nurseries and restoration projects. The source of this poor germination response has not been identified. However the data presented here clearly shows that a significant portion of the seed population—as much as 65%—will never germinate because they lack embryonic or endosperm tissues, or the embryos

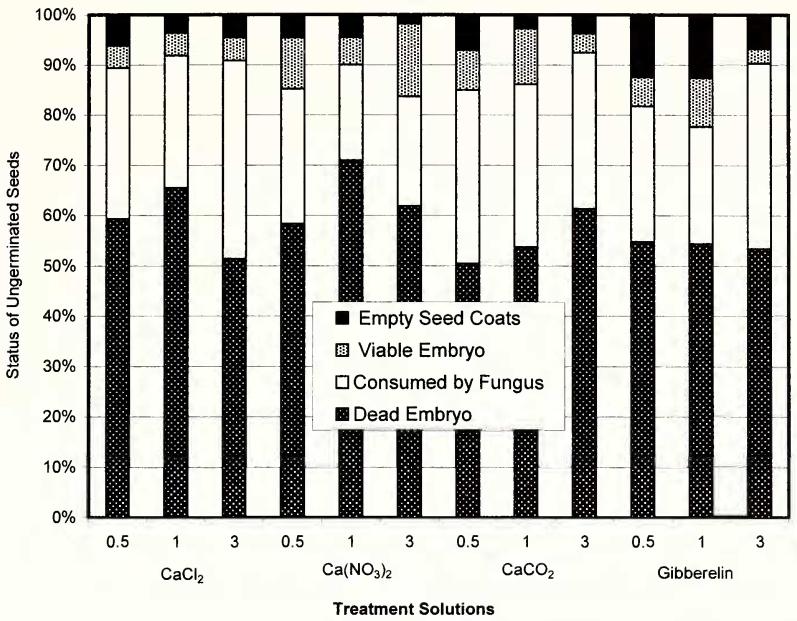

FIG. 4. Status of ungerminated seeds after chemical treatment and 10 day incubations. Ungerminated seeds were scored for fungal contamination. Seeds with little or no contamination were dissected and treated with 0.5% tetrazolium of determination of embryo viability.

are not metabolically active. Under horticultural conditions, a significant portion of the population also succumbed to fungal infection. It is possible that infection was enhanced by the absence of viable embryo. The data further suggest that some portion of the seeds identified as viable prior to planting, lost viability during the germination test. The reason for this remains unclear.

Cool storage temperatures significantly increased germination of seeds that had been held for 6

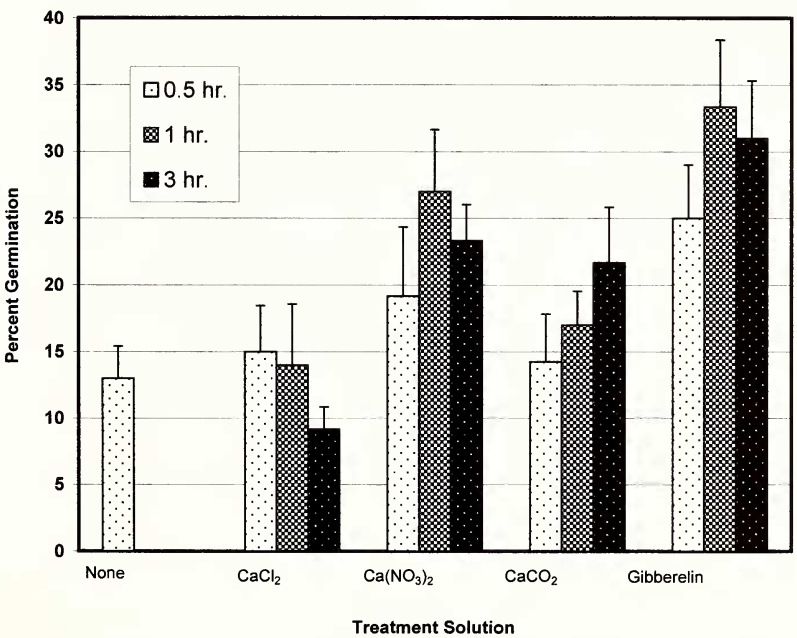

FIG. 5. Evaluation of chemical treatments and exposure times for enhanced germination of *Encelia farinosa* seeds planted in vermiculite and grown in the glasshouse. Data shown are from commercially available seeds stored under cold conditions. Similar responses were observed for seeds collected from local sites.

months or more. Cool storage serves two functions: the reduced temperatures slow metabolic activity of both seeds and infectious microbes and secondly, cool temperatures contain less water. The dryer the atmosphere, the longer a seed retains its dormant condition (Bewley and Black 1994). When seeds are exposed to cool, *moist* conditions such as refrigeration storage in damp peat moss, stratification can occur. This common seed treatment is most effective for temperate species and is thought to preclude early germination until the correct environmental signal is received to indicate spring (Bewley and Black 1994). *Encelia farinosa* is not known to respond to stratification, and because seeds were not stored in this manner, we do not believe that the enhanced germination of the cold-stored seed was due to stratification. However, the possibility of a dry chilling requirement in this species has not been evaluated and cannot be ruled out at this point.

Of the seeds stored under cool conditions a consistent 30% from each of three pooled populations contained seeds with non-viable embryos. Significant portions of the remaining seeds were only empty seed coats leaving the viable population between 30% and 50%. It should be noted, however, that this determination was made from a visually inspected and uniform population of seeds. These populations were specifically selected as undamaged, and representative of the healthy population mean in terms of size and weight. The seeds that were rejected during inspection were not accurately counted, but we estimate a percentage of about 25% were unsuitable because of insect predation, broken seed coats, or size and mass outside of the population mean. When this is taken into account (and assuming that the rejected seeds would not have germinated), maximum germination percentages from the bulk population are expected to be between 20% and 40%, if every viable seed sprouted.

Untreated germination percentages were about 5% for seeds tested in petri dishes and 12% for seeds evaluated in vermiculite (control bars in Figs. 3 and 5). Gibberellic acid significantly increased the germination percentages in all of the experiments under all conditions. The application of the plant growth regulators gibberellin, cytokinin, and ethylene to break dormancy is widely recognized (Powell 1988). Of the three, gibberellin is the most commonly used and frequently substitutes for other germination signals such as light and chilling requirements. However, not all plants respond to gibberellin (Powell 1988, Bewley and Black 1994). In cereal grains, applications of gibberellic acid stimulate the activity of several enzyme systems including the initiation of hydrolysis of starch to glucose. Other plant families seem to respond to applications of gibberellic acids with changes in enzyme activity, but the numbers of species investigated is quite limited (Jacobsen and Chandler 1988, Bewley and Black 1994). During cell development exogenous applications of gibberellic acid stimulates cell elongation (Métraux 1988). Given the observation that *Encelia farinosa* does not respond to stratification, nor seems to have any specific light requirements, it seems reasonable to surmise that the germination responses to gibberellic acid is due to induced enzyme activity.

The germination rate was clearly better in vermiculite as compared to petri dishes (Figs. 3 and 5), but both methods were superior to the germination percentages of seeds planted in artificial potting media or native soils (data not shown). There were many environmental differences between these two methods, and as a rule the goals of these two methods were different. Vermiculite provides no substantial nutrient source (Troeh and Thompson 1993), but the greenhouse environment provided more light, better aeration, and most likely more compatible moisture regime suitable for transplanting germinated seedlings for establishment. While petri dish methods are rarely used for establishment of potted plants, they are often used to estimate viable seed content. We did not attempt to optimize the incubator conditions used for the experiments and it is likely that other parameters may have increased seedling yield. In any event the relative responses to the seed treatments remain consistent between the two methods even if the total germination varied.

We found that it was nearly impossible, based on microscopic observation of undissected seeds or mass of dried seeds, to predict which individuals would contain a viable embryo. The dried seeds, when harvested or as released from the flower head, are very flat but swelled rapidly with imbibition. Unfortunately, even seeds without an embryo or an endosperm often swelled with imbibition. Also, there was no consistent relationship between seed viability and position on the flower head (data not shown). Many of the outer-most and innermost seeds were underdeveloped, but these were usually eliminated during visual inspection. We could devise no method for identifying and selecting viable seeds prior to planting.

The adaptive advantage of this poor seed set under natural conditions is unclear. A typical *Encelia farinosa* shrub produces tens of thousands of seeds. Perhaps by hiding the "good" seeds among the "bad" seed, the viable seeds are more likely to escape predation. It seems unlikely that this is the result of environmental conditions because of the two field sites. Box Springs Mt. is the more highly disturbed and influenced by urban pollution (Allen et al. 1997). Yet, Box Springs Mt. had the more viable population of viable seeds. Although the history of the commercial seeds is unknown, we assume that they were collected from relatively pristine desert populations. Other than the greater percentage of empty seed coats observed from the Lake Skinner seeds, all three sources behaved remarkably similarly.

In conclusion: the most significant cause of the poor germination in *Encelia farinosa* is lack of viable embryos in nearly 50% of the seeds tested. Storage at 5° to 10°C resulted in better germination percentages than seeds stored at room temperature. Soaking the seeds in 0.1% gibberellic acid for 30 minutes to 1 hour at 37°C improved germination by about 2 fold as compared to no treatment. And finally germination in horticultural vermiculite followed by transplantation into sterile potting media resulting in about 30% germination and a successfully reared population of seedlings.

Acknowledgments

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